Local and Landscape Influence on Red-winged Blackbird (*Agelaius phoeniceus*) Nest Success in Great Lakes Coastal Wetlands

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ABSTRACT: Nest predation has been identified as the primary mechanism contributing to reduction of reproductive success for the marsh-breeding red-winged blackbird (Agelaius phoeniceus). *Differences in rates of nest predation have been linked to nest site characteristics within a wetland, primarily water depth. However, the relationship between the landscape surrounding these habitats and the probability of nest predation is uncertain. Moreover, factors associated with reproductive success could be a potentially powerful indicator of ecological condition in wetland habitats. We investigated the influence of landscape pattern on nest success by monitoring 366 red-winged blackbird nests in 11 coastal wetlands along the south shore of Lake Superior. Of the 366 nests, 39% were successful, 56% failed, and 5% were abandoned or lacked sufficient evidence to determine nest fate. Nest predation accounted for over 93% of total failures. Predation rates ranged from 31% to 97% among the 11 wetland sites. We modeled nest predation using multi-model logistic regression analysis and the Akaike information criterion to identify and parameterize influential variables derived from the nest site, wetland, and landscape surrounding each wetland. Our results indicated that landscape variables comprised over 50% of model prediction weight in 15 of the 17 models. Nest failure was highest at sites within an urban/residential landscape matrix. Reproductive success could be a good indicator of the ecological health of Great Lakes wetlands.*

INDEX WORDS: Agelaius phoeniceus, *nest predation, Great Lakes wetlands, indicator.*

INTRODUCTION

Nest predation studies in wetland landscapes have emphasized the importance of water depth for predicting nest fate (Robertson 1972). For example, Picman (1988) found lower nest predation rates in marshes than in upland habitat and hypothesized that low predation rates in the marsh were due to nest inaccessibility. Later, Picman *et al.* (1993) found that predation and predator diversity decreased as water depth increased. Again, water depth was thought to make marsh nests more difficult for terrestrial predators to reach. In a similar fashion, Jobin and Picman (1997) found that passerine nest success was best predicted by water depth in urban and natural marshes where terrestrial

predators were thought to dominate the predator assemblage. However, nest concealment and vegetation density were more important predictors in agricultural marshes where Jobin and Picman (1997) attributed nest losses to avian predators such as marsh wrens (*Cistothorus palustris*) and common grackles (*Quiscalus quiscula*).

This discrepancy between the influence of water depth and nest concealment on nest success in differing wetland contexts, suggests that the importance of nest-site and wetland characteristics are influenced not only by their interaction with local predator assemblages and vegetation structure, but also by patterns at the landscape scale. Landscape composition and wetland characteristics may favor certain predators, thereby influencing rates of nest predation in wetlands. Landscape-level studies of avian communities in wetland habitats have attempted to elucidate the connection between community composition and wetland size (Brown and

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Dinsmore 1986, Craig and Beal 1992), wetland isolation (Brown and Dinsmore 1986, Fairbairn and Dinsmore 2001), and connectedness and road density (Whited *et al.* 2000). However, these studies did not explicitly examine the influence of landscape pattern on nest predation. Therefore, we analyzed the influence of both local (i.e., nest and wetland characteristics) and landscape characteristics on red-winged blackbird nests in 11 wetlands along the south shore of Lake Superior, U.S.

The goal of the study was to assess the connection between predation rates and landscape pattern. We conducted an exploratory analysis to answer two questions:

1. In what manner do local and landscape characteristics contribute to the probability of nest predation?
2. What is the relative importance of landscape variables compared with local variables?

By gaining a better understanding of factors associated with nest success of birds using coastal wetlands, we can determine whether bird reproduction can be used as a potential indicator to assess detrimental changes in these systems (Niemi and McDonald 2004). We use the red-winged blackbird as a potential model organism to examine these questions because it is a ubiquitous and abundant species found in these wetland ecosystems and its nests are relatively easy to find.

METHODS

Study Sites

Eleven coastal wetlands were chosen along the south shore of Lake Superior between Duluth, Minnesota and Ashland, Wisconsin (Fig. 1). Study sites were chosen based on the availability of suitable red-winged blackbird habitat, namely herbaceous wetlands dominated by cattail (*Typha latifolia*) and sedge (*Carex* spp.). The 11 sites ranged between 3.81 and 13.79 ha (mean area = 8.5 ha) in size.

Nest-site Variables

Systematic nest searching efforts were conducted during the breeding season in each wetland site from 20 May 02 to 1 Aug 02. Field crews searched all suitable nesting habitat in each wetland with an emphasis on finding all red-winged blackbird nests. Searches were conducted every 3 to 5 days in each

wetland. Each nest was given a unique identification number, flagged at a distance no closer than 5 m, and notes were taken to aid in relocation. Water depth (Picman 1988, Picman *et al.* 1993), categorical estimate of vegetation density within 5 m of each nest (Jobin and Picman 1997, Martin *et al.* 1997), overhead concealment (Jobin and Picman 1997), and distance to wetland edge (Kuehl and Clark 2002) were measured at each nest location. We are confident that we found > 90% of all red-winged blackbird nests in each wetland. This is based on frequency and intensity of our nest searching efforts, plus the size of the wetlands sampled. In all cases it would have been unlikely to not find nests prior to nest failure or abandonment by the adults.

Nests were visited every 3 to 5 days until the nesting cycle was terminated as young fledged or nests failed. Success was defined as at least one juvenile fledging from a given nest and failure as the complete loss of nest contents or nest abandonment after partial nest loss to predation. At each visit, nest contents and parental activity were recorded. Precautions were taken to avoid disturbing adults near or at the nest, destroying vegetation around the nests, or forming dead-end trails to nest sites (Olson and Rohwer 1998). We scanned wetlands for the presence of potential predators (crows, cowbirds, raccoons, etc.) before entering the wetland to conduct nest visits. If predators were detected, the check was postponed until the predators were no longer observed in the wetland or along the wetland edge. Nest success was calculated using the Mayfield estimation method (Mayfield 1975, Johnson 1979). Only nests with known fates were included in the analysis. Predation rates for each wetland were therefore equal to 1 minus the respective success rate.

Wetland-level Variables

Within each wetland, 10 randomly located 200 m transects were established to detect and identify avian predators. Transects were positioned such that at least half of each transect would be located within the emergent vegetation zone of the wetland. Observers walked along each transect, recording visual and auditory detections of potential avian predators. We established two indices based on total detection frequency over the ten transects in each wetland; the first described the number of active potential avian predators, including American crow (*Corvus brachyrhynchos*), blue jay (*Cyanocitta*
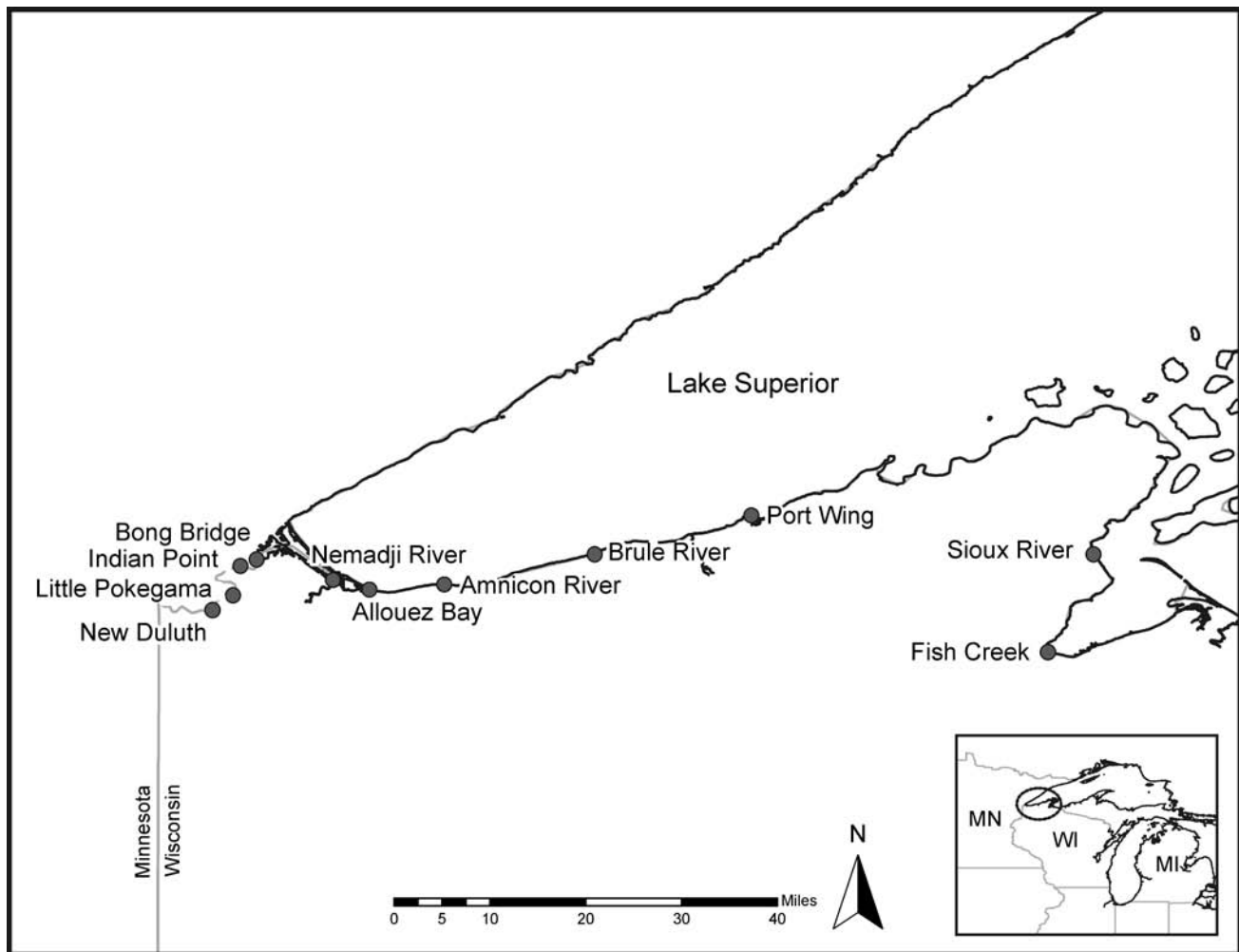
FIG. 1. Location of study region and 11 study sites along the south shore of Lake Superior, USA.

cristata), common grackle, marsh wren, and sedge wren (*Cistothorus platensis*). The second index described the number of active brown-headed cowbirds, which have been reported to remove eggs and kill nestlings (Arcese *et al.* 1996, Granfors *et al.* 2001).

Red-winged blackbird nest density (thought to influence nest predation through the anti-predation benefit of communal nest defense [Picman *et al.* 1988, Searcy 1988]) and wetland area (shown to positively influence species richness [Brown and Dinsmore 1986, Craig and Beal 1992]) were also examined as potential explanatory variables in our logistic models.

Landscape Variables

We assessed the landscape configuration within a 1 km radius buffer around each wetland's centroid using the FRAGSTATS software package (McGarigal and Marks 1995). We used the National Land Cover Dataset classification system (Vogelmann *et al.* 2001) to characterize each wetland landscape, defined by the 1 km radius buffer. For each wetland landscape, total area was calculated for each cover class found within the 1 km buffer as the basis for quantifying landscape composition. Total area for each cover class within the 1 km buffer was then converted to a percentage of total landscape area of that buffer (314.16 ha). We chose a subset of FRAGSTATS metrics that included percent residential, industrial, deciduous forest, and wetland cover in each landscape to represent landscape composition.

We calculated two additional metrics for inclusion in landscape analysis, wetland isolation, and road density. Wetland isolation was defined as the

TABLE 1.   Summary of nest site characterization for each wetland site.

Variable	Abrv	Units	Mean	Std. error
Water depth	wat_d	meters	0.1	0.2
Distance to edge	dist_e	meters	32.4	23.0
Percent overhead concealment	over	percent	11.1	19.6
Vegetation density (within 5 m radius of nest)	dens	low, med., high	2.0	0.7
Wetland area	area	Hectares	8.5	3.2
Nest density	nest_d	number/hectare	4.7	2.2
Index of avian predator activity	a_pred	number detected	13.2	5.5
Brown-headed cowbird activity	bhco	number detected	7.0	12.2
Road density	road_d	meters/hectare	30.6	23.4
Percent total residential	ptr	percent	9.4	11.8
Percent commercial, industrial and transportation	pcit	percent	11.2	15.9
Percent deciduous forest	pdf	percent	16.4	16.6
Percent total wetland	ptw	percent	19.0	20.2
Distance to nearest wetland	dist_nm	meters	1,675.7	1,427.0

average distance (in m) from the edge of the focal wetland to the two nearest wetlands greater than 0.2 ha (Whited *et al.* 2000). To examine the influence of road density on nest predation, we imported the Tiger road datasets (Census 2000) for Minnesota and Wisconsin into ArcView and examined the data for roads within each 1 km landscape. All roads (i.e., highways, residential roadways, dirt roads) were included in calculations of total road density (m of roads per ha) since the diversity of road types varied little among wetland buffers.

Statistical Analysis

With the combined set of nest site, wetland, and landscape metrics as potential explanatory variables (Table 1), we constructed a suite of logistic models to examine their relationship to the probability of nest predation. An exploratory approach was taken to identify potential factors that could be the focus of future experimental investigations. Local and landscape variables were standardized to a z-distribution to make the units dimensionless, allowing for direct comparison among regression coefficients. We used best subset selection (Hosmer *et al.* 1989) to generate a list of logistic regression models using PROC LOGISTIC (SAS Institute Inc. 1995). The three models with the highest likelihood score in each group, differentiated by the number of variables along with the global model, which included all 14 variables, were retained for analysis (SAS Institute Inc. 1995). As a result, 40 logistic models were generated with the dependent variable, in this case failure and success, coded as 0 and 1, respectively.

Overall fit for the global model was assessed using the Hosmer and Lemeshow (2000) goodness-of-fit test. Overdispersion for the global model was examined using the variance inflation factor $\hat{c}$, calculated by dividing the Hosmer and Lemeshow goodness-of-fit statistic by its degrees of freedom (Burnham and Anderson 1998). The most likely causes of overdispersion come from lack of fit due to model misspecification and violation of independence among observations (Allison 1999). The auto-correlated nature of nest success data (e.g., neighboring nests are more likely to share the same fate than nests in other wetlands), therefore, necessitated an assessment of overdispersion prior to model comparison.

We used the small sample correction for Akaike's information criterion (AIC_c; Hurvich and Tsai 1989, Burnham and Anderson 2001) to rank candidate models. AIC_c difference (Δ_i) and Akaike weight (w_i; Buckland *et al.* 1997) were calculated for each model to assess model uncertainty and the likelihood of each candidate model given the data. We considered models with $\Delta_i \leq 2$ to be well supported by the data (Burnham and Anderson 2001).

We used this subset of models to assess parameter importance by summing Akaike weights for the models containing a given parameter. This yielded the predictor weight for each parameter based on the set of supported models (Burnham and Anderson 1998). The parameter with the largest predictor weight was considered the most important (Burnham and Anderson 1998). In addition, we calculated an estimate of the unconditional variance and 95% confidence intervals for each parameter esti-

TABLE 2.　Summary of wetland patch characterization.

Site name	Wetland size (ha)	Number of nests	Median vegetation density	Avg. depth (m)	Avg. overhead concealment (%)	Avg. distance to wetland edge (m)
Allouez Bay	7.12	27	1.00	0.14	32.8	39.6
Amnicon River	6.45	27	1.00	0.17	19.8	24.8
Bong Bridge	13.79	59	2.00	0.08	5.5	24.3
Brule River	8.84	10	1.00	0.18	10.5	16.6
Fish Creek	13.26	45	1.00	0.10	7.8	44.5
Indian Point	7.85	60	2.00	0.09	7.5	39.0
Little Pokegama	6.03	10	2.00	0.04	7.5	45.4
Nemadji	7.10	25	2.00	0.17	15.8	34.8
New Duluth	11.85	30	2.00	0.13	14.0	21.2
Port Wing	3.82	34	2.00	0.19	7.5	30.6
Sioux River	7.07	22	1.00	0.11	3.4	29.2

mate (Buckland *et al.* 1997, Burnham and Anderson 1998).

RESULTS

Nest-site Variables

A total of 366 red-winged blackbird nests were located. Nesting activity occurred from 15 May to 31 July. Brule River and Little Pokegama Bay contained the fewest nests (*n* = 10) while over 20 nests were found at each of the remaining sites. Average vegetation density was similar among wetland sites, as was average water depth with the exception of Little Pokegama Bay which was the driest site included in the study (Table 2). Overhead conceal-

ment varied considerably among sites with the Sioux River having the lowest average concealment and Allouez Bay the highest (Table 2). In addition, the average distance from the nests to the wetland edge was similar among each of the 11 wetlands (Table 2).

Seventeen of the 366 nests were eliminated from further analysis for the following reasons: 1) 12 nests lacked sufficient evidence to determine nest fate or cause of nest failure, 2) three nests were abandoned, and 3) two nests were lost to flooding. Storm events did not play a significant role in the loss of nests based on field observation. The remaining 349 nests were used to estimate nest success over 4,878 exposure days (Table 3). Predation

TABLE 3.　Mayfield estimates of success and failure for red-winged blackbird (**Agelaius phoeniceus**) *nests found in wetland sites along the south shore of the western arm of Lake Superior, USA.*

| Wetland	Exposure days	Depredated nests	Total nests	Losses per nest day	Success rate(s)	Standard error(s)	Predation rate (*p*)
Allouez Bay	492	8	27	0.016	0.69	0.0057	0.314
Amnicon River	425	11	27	0.026	0.55	0.0077	0.453
Bong Bridge	392	55	59	0.140	0.03	0.0175	0.969
Brule River	147	5	10	0.034	0.45	0.0150	0.550
Fish Creek	511	35	45	0.069	0.20	0.0112	0.805
Indian Point	919	38	60	0.042	0.37	0.0067	0.631
Little Pokegama	176	5	10	0.028	0.51	0.0126	0.486
New Duluth	518	10	30	0.019	0.64	0.0061	0.362
Nemadji	422	13	25	0.031	0.49	0.0084	0.514
Port Wing	499	16	34	0.032	0.47	0.0079	0.527
Sioux River	381	9	22	0.024	0.58	0.0078	0.423
Totals:	4,878	205	349				
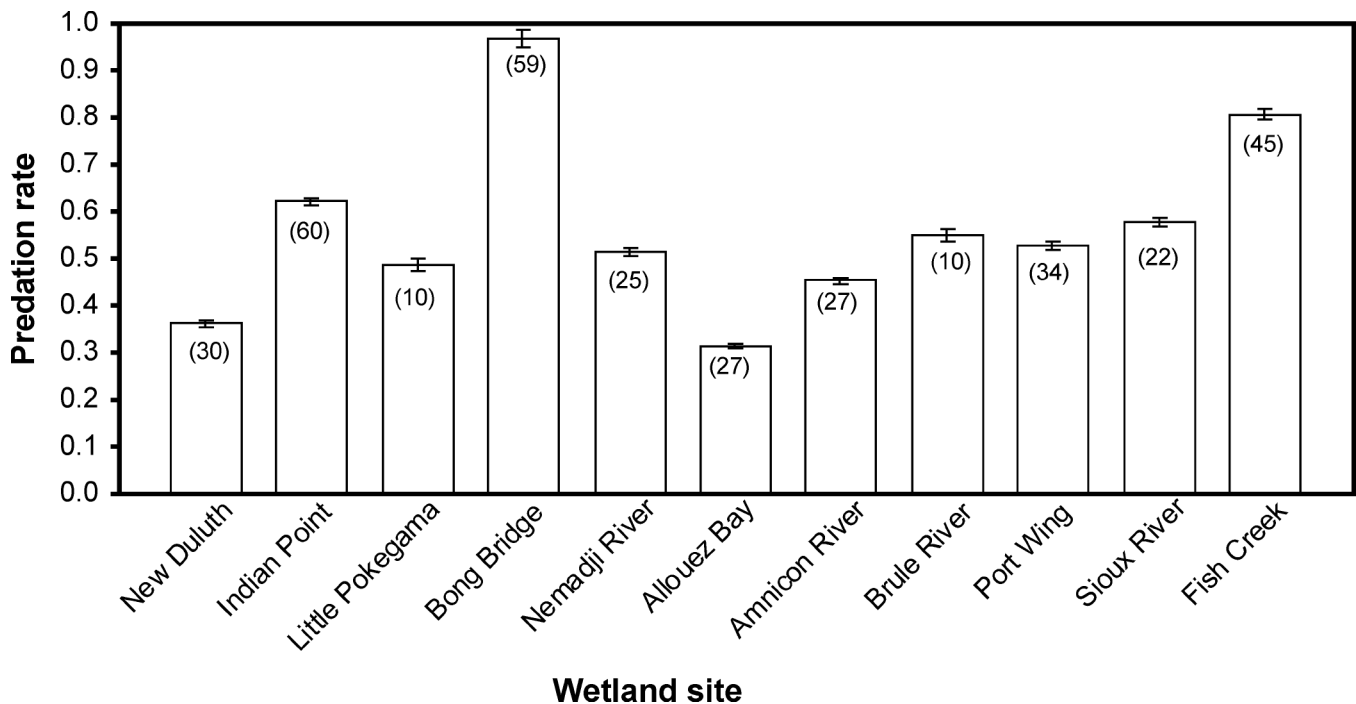
FIG. 2. *Proportion of red-winged blackbird* (**Agelaius phoeniceus**) *nests lost to predation in each wetland (± SE). Number in parentheses represents the number of nests monitored at each site.*

accounted for 93% of 205 nest failures. Predation rates ranged from 31% to 97% with a mean of 55% among the 11 wetland sites (Fig. 2). Allouez Bay had the lowest rate of predation while Fish Creek and the Bong Bridge had the highest rates of predation. We found no evidence of brown-headed cowbird parasitism despite their presence at many of the study sites.

Unsuccessful nests were categorized by nest appearance and egg or nestling remains after predation (Fig. 3). Fifty-five percent of predation events involved the complete removal of nest contents without noticeable damage to the nest itself. Approximately 30% of the nests were damaged while close to 15% were completely destroyed. Egg fragments were discovered in or near nests in nearly 15% of the total predation events. The nest lining was pulled up or completely removed in 12%. Overhead and surrounding vegetation was damaged in 5% of the nests lost to predation. One nest had a pencil-sized hole in the bottom of the cup.

Wetland-Level Variables

A total of 182 potential predators, among seven species, were detected during predator surveys (Table 4). Blue jays were the most frequently de-

tected species followed closely by brown-headed cowbirds, American crows, and sedge wrens. Less common species included common grackle and marsh wren. The Bong Bridge site had the greatest number of predators, whereas the Amnicon River and Indian Point sites had the fewest (Table 4). The Bong Bridge had the greatest number of brown-headed cowbird sightings, followed by Little Pokegama and Nemadji River. Three brown-headed cowbirds were detected at New Duluth and one each at Allouez Bay and Sioux River Slough. One raccoon (*Procyon lotor*) was observed moving through a densely nested area at the Bong Bridge site. Other potential mammalian predators whose scat or tracks were detected along predator transects included black bear (*Ursus americanus*), unknown canid (*Canus* sp.), and domestic cat (*Felis catus*). We also detected whitetail deer (*Odocoileus virginianus*), which have recently been identified as nest predators in grassland ecosystems (Pietz and Granfors 2000). However, the limitation of our predator transects to detect mammalian predators, which are most active during the night, resulted in too few mammalian predators being detected to allow statistical analysis of the non-avian contribution to overall predator activity.
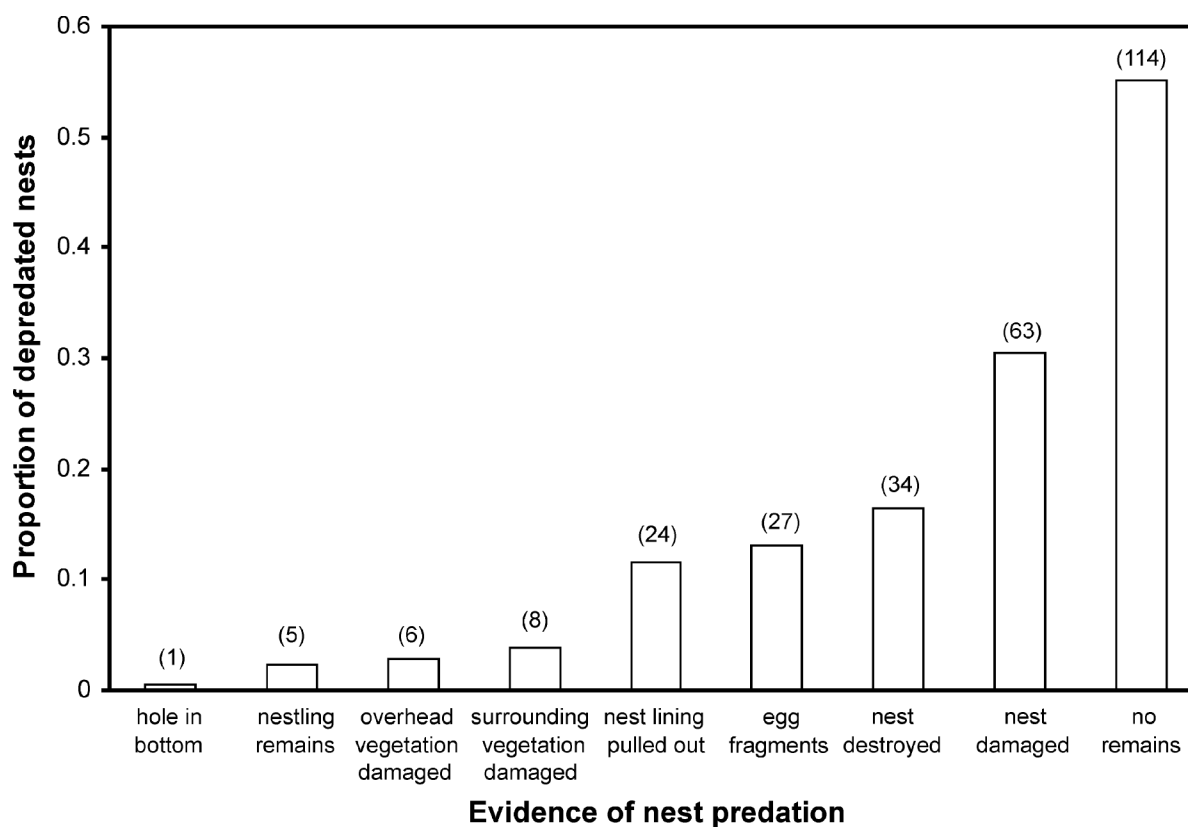
FIG. 3.   *Depredated nests categorized by nest appearance and egg or nestling remains. Categories are not mutually exclusive. Number in parentheses indicates the frequency for each category.*

Detected nest density averaged 4.7 nests per ha. Wetland area varied among sites, ranging from 3.81 to 13.79 ha (Table 2).

Landscape Variables

The proportion of the surrounding landscape devoted to development averaged 20.6% (residential = 9.4%; commercial, industrial, or transportation = 11.2%) across the 11 wetland sites (Table 1). Individually however, development was generally low in the surrounding landscape (Table 5) with the exception of the Bong Bridge, Nemadji, Indian Point, and Port Wing which had a larger proportion of the landscape dedicated to human development. Deciduous forest cover generally accounted for the largest proportion of the landscape within the defined buffer and the amount of wetland cover varied among sites but comprised no more than 55% of any wetland landscape (Table 5). Port Wing was the most isolated site. Road density varied considerably

among sites, ranging from 3 to more than 60 m per ha.

Statistical Analysis

The global model with 14 parameters and an intercept (model 40; Table 6) provided an acceptable fit to the data (P > 0.5). We found no overdispersion ($\hat{c} = 1.04$), providing evidence that the assumption of independence among nests was not violated. Eleven models made the $\Delta_i < 2$ cutoff for consideration as potential best approximations given the data (Table 6). The weight of evidence (w_i) of the four models with the lowest Akaike difference was twice as strong as the remaining thirteen models in the candidate set. The top four models contained similar parameters including overhead concealment, vegetation density, road density, percent residential and commercial development, and percent wetland cover. However, the weight of evidence for any of these four models was not convincingly strong

TABLE 4. *Predator detections along 10, 200 m transect surveys.*

Site name	Blue Jay	Brown-headed Cowbird	American Crow	Sedge Wren	Common Grackle	Marsh Wren	Total
Allouez Bay	1	1	0	13	5	0	20
Amnicon River	6	0	0	1	0	0	7
Bong Bridge	0	17	11	1	6	0	35
Brule River	9	0	0	15	0	0	24
Fish Creek	9	0	4	0	0	0	13
Indian Point	3	3	0	0	1	0	7
Little Pokegama	5	9	10	1	0	0	25
Nemadji	0	8	2	1	0	0	11
New Duluth	0	3	2	3	0	0	8
Port Wing	7	0	5	0	0	3	15
Sioux River	5	1	6	5	0	0	17
Total	45	42	40	40	12	3	182

(Table 6), indicating a substantial amount of model selection uncertainty.

Weighted average parameter estimates along with unconditional standard errors for all parameters included in the suite of possible approximating models were ranked in order of increasing importance based on the summation of Akaike weights for all models in which they appear (Table 7). Seven variables were distinguished from the remaining variables by a large difference in cumulative parameter weight (Table 7). However, the 95% confidence interval for vegetation density, distance to edge, and water depth included 0.

DISCUSSION

Local Variables

Our modeling suggests that nest site vegetation is an important component in protecting the nest from predation. Both overhead concealment and vegetation density had high predictor weight, suggesting a strong negative influence on the probability of predation. Jobin and Picman (1997) found nest concealment and vegetation density to be important predictors of nest success in agricultural marshes where the primary threats to nest success were avian predators. Red-winged blackbirds generally selected dense stands of emergent vegetation, when available, for nest sites. This may increase the number of possible nest sites, impede the movement of some predators (Bowman and Harris 1980), and conceal parental activity often used as a cue for visually oriented predators in nest detection (Holoway 1991).

Despite the high degree of importance placed on water depth in previous wetland nest predation studies (Robertson 1972, Picman *et al.* 1993, Jobin and Picman 1997, Özesmi and Mitsch 1997), our results

TABLE 5. *Summary of landscape analysis.*

Site name	% Residential	% Industrial	% Deciduous forest	% Wetland	Distance to nearest wetland (m)	Road density (m/ha)
Allouez Bay	0.0	0.9	29.6	3.9	861.7	6.5
Amnicon River	0.0	1.0	49.0	2.0	3,652.0	12.4
Bong Bridge	16.2	44.6	2.2	3.3	1,800.0	57.8
Brule River	0.0	0.3	29.9	1.4	2,937.3	7.0
Fish Creek	0.0	0.3	0.5	52.9	676.0	3.4
Indian Point	30.0	14.0	10.7	5.5	801.0	61.7
Little Pokegama	0.1	0.0	58.9	2.6	1,095.0	11.9
Nemadji	20.6	9.2	13.1	21.0	889.7	47.2
New Duluth	0.0	3.0	39.9	22.3	325.3	13.0
Port Wing	60.0	1.2	3.5	55.0	5,111.3	23.9
Sioux River	0.0	0.3	17.8	20.7	1,421.3	16.0

TABLE 6. Candidate predation probability models number of estimable parameters (K) second order Akaike's information criterion (AICc) Akaike difference (AIC), and Akaike weight (wi).

Model	Variables	K	AICc	ΔAIC	wi	% wi local	% wi land
1	intercept, over, dens, dist_e, road_d, ptr, pcit, ptw	8	406.6	0.00	0.129	40	60
3	intercept, over, dens, road_d, ptr, pcit, ptw	7	406.8	0.18	0.118	33	67
2	intercept, over, dens, dist_e, road_d, ptr, pcit, ptw, dist_nm	9	406.9	0.28	0.112	37	63
4	intercept, over, dens, road_d, ptr, pcit, ptw, dist_nm	8	407.1	0.45	0.102	30	70
5	intercept, over, dens, dist_e, road_d ptr, pcit, ptw, area	9	408.3	1.64	0.057	41	59
11	intercept, over, road_d, ptr, pcit, ptw, dist_nm	7	408.3	1.70	0.055	19	81
8	intercept, over, dens, dist_e, road_d, ptr, pcit, ptw, wat_d	9	408.4	1.73	0.054	42	58
10	intercept, over, dist_e, road_d, ptr, pcit, ptw, dist_nm	8	408.4	1.74	0.054	28	72
6	intercept, over, dens, dist_e, road_d, ptr, pcit, ptw, dist_nm, nest_d	10	408.5	1.83	0.052	37	63
7	intercept, over, dens, dist_e, road_d, ptr, pcit, ptw, dist_nm, wat_d	10	408.5	1.83	0.051	38	62
9	intercept, over, dens, dist_e, road_d, ptr, pcit, ptw, dist_nm, bhco	10	408.5	1.88	0.050	38	62
12	intercept, over, road_d, ptr, pcit, ptw	6	408.7	2.11	0.045	21	79
13	intercept, over, dens, dist_e, ptr, dist_nm, area	7	409.3	2.67	0.034	63	37
14	intercept, over, dens, dist_e road_d, ptr, pcit, ptw, dist_nm, nest_d, wat_d	11	409.9	3.31	0.025	39	61
15	intercept, over, dens, dist_e, road_d, ptr, pcit, ptw, dist_nm, wat_d, bhco	11	410.0	3.41	0.023	39	61
16	intercept, over, dens, dist_e, road_d, ptr, dist_nm, area, wat_d, bhco, pdf	11	410.3	3.68	0.020	46	54
17	intercept, over, dist_e, pcit, area, pdf	6	410.4	3.79	0.019	64	36
40	intercept, over, dens, dist_e, road_d, ptr, pcit, ptw, dist_nm, area, nest_d, a_pred, wat_d, bhco, pdf	15	416.6	9.93	0.001		

indicated that water depth had a marginal effect on nest fate. However, these results may have been an artifact of the low variability of water depth within and among sites. This lack of variation created a natural "experiment" where water depth was essentially held constant. Under this scenario, we would expect water depth to exhibit minimal influence on predation while other factors (e.g., overhead concealment) would have greater impact. Picman and Schriml (1994) found that predator assemblages varied among habitats and that wetlands had lower predator diversity than adjacent upland areas because deeper water prevented terrestrial predators from accessing wetland nests. Given the low variation in water depth during our study, we might expect lower variation in the terrestrial predator assemblage and a greater proportion of the variability in predation rates to be attributed to nest-site characteristics influencing predation by avian predators. Without a thorough examination of the predator assemblage, we can only speculate to the composition of the terrestrial and avian predator assemblage.

TABLE 7. Variable importance arranged by declining predictor weight and parameter estimates with their standard error and 95% confidence intervals.

Variable	Predictor weight	Parameter estimate	Standard error	Upper CI	Lower CI
Overhead concealment	1.00	–0.45	0.14	–0.18	–0.73
% Total residential	0.98	1.59	0.71	3.02	0.17
Road density	0.95	–1.95	0.84	–0.27	–3.62
% Commercial, industrial, transportation	0.95	1.70	0.40	2.50	0.89
% Total wetland	0.93	0.39	0.14	0.67	0.11
Vegetation density	0.83	–0.22	0.12	0.02	–0.45
Distance to edge	0.68	0.14	0.10	0.34	–0.06
Water depth	0.17	–0.01	0.02	0.03	–0.06

Wetland-level Variables

The index for total predator activity did not enter into any of the predation probability models. This suggests that the identity of specific predators and their mode of predation may be more important than the combined activity of the entire predator assemblage. Rather than combine predator species into one index, it may be more important to focus on predator response to landscape pattern (Chalfoun et al. 2002). Picman et al. (1993) demonstrated that relatively few predator species were responsible for nest predation in wetlands, and aggregating predator species may mask the effects of a particularly influential predator.

Landscape Variables

We found the pattern of the surrounding landscape has a substantial influence on nest success in coastal wetlands. The proportion of residential and industrial development in the surrounding landscape had a particularly strong positive influence on the probability of nest failure due to predation. These landscapes may foster a diverse assemblage of avian and terrestrial predators by providing supplemental food resources, which facilitate artificially high predator densities (Marzluff et al. 1998), and introducing non-native and human associated predators such as house cats (Soulé et al. 1988, Crooks and Soulé 1999). Although many upland regions surrounding these coastal wetlands have a relatively low degree of development, those with high levels (e.g., Bong Bridge, Indian Point) exhibited the highest rates of predation. Although the red-winged blackbird is not a species of conservation concern, with growing regional development (Orr 1997), predation impacts identified for the red-winged blackbird will likely extend to other marsh breeding birds in these systems. Hence, the species continues to have potential as an indicator of reproductive success for wetland bird species in the coastal wetlands. Most bird species in these wetlands are too rare or their nests are too difficult to find to be of practical use as indicators of reproductive success.

Recent reviews by Spellerberg (1998) and Trombulak and Frissell (2000) detail the effects of roads, pointing to their deleterious influence on natural ecosystems. For example, Whited et al. (2000) found that increasing road density decreased avian species richness. In this study, high road densities were associated with a low probability of predation. Roads may impede the movement of terrestrial wetland predators in forest dominated ecosystems through road avoidance and direct mortality, thereby reducing the predation pressure in nearby wetlands. Road avoidance has been documented for small forest mammals (Oxley et al. 1974) and several large mammals (Brody and Pelton 1989, Thurber et al. 1994), although roads may facilitate predator movement in some instances. However, predators that utilize transportation corridors will also be more susceptible to direct mortality due to traffic. Roads are less likely to restrict the movements and home ranges of avian predators and may, in some instances, attract avian predators to the transportation corridor (e.g., ravens [*Corvus corax*], Knight and Kawashima 1993). As a result, predator assemblage may become dominated by avian predators which are thought to account for most predation events in deep water wetland habitats (Picman and Schriml 1994, Jobin and Picman 1997).

The probability of nest predation increased with the proportion of wetland in the landscape. Wetland dominated landscapes may support predator assemblages dominated by wetland adapted predators. More wetland habitat could also support higher nest densities, thereby increasing nest predation efficiency through a numerical response by predators.

Highly fragmented landscapes with many small wetlands are likely to influence predation probabilities differently than landscapes with large contiguous wetlands (Chalfoun et al. 2002). Gibbs (1993) showed that removing small wetlands from the landscape increased the extinction probabilities of local populations of small mammals, birds, salamanders, turtles, and frogs.

Predator densities may be higher in more contiguous wetland complexes. A high degree of background fragmentation in the surrounding matrix may drive predators towards coastal wetlands, which generally receive stronger legal protection than other habitats in the surrounding landscape including inland wetlands (Greiner la Peyre et al. 2000). Additionally, fragmented wetland complexes may be associated with high avian predator activity (Chalfoun et al. 2002), a phenomenon consistently documented in forested systems (Yahner 1988). The positive response of avian predators to fragmentation (Chalfoun et al. 2002) is likely the result of edge adapted species hunting along habitat edges. In the case of coastal wetlands and adjacent deciduous dominated forest ecotypes, these edges are especially distinct. However, we found that predator activity did not vary with fragmentation.

Isolation has been implicated as an important

variable influencing species richness (Brown and Dinsmore 1986), but its marginal contribution to the predictive ability of the models suggests the effect of wetland isolation on nest predation in coastal wetlands is negligible. Character of the surrounding matrix may impede or facilitate predator movements across the landscape depending on species-specific dispersal characteristics. As with edge effects (Donovan *et al.* 1997), there may be geographical variation in the direction of the influence of wetland isolation on predator assemblages, and wetland predators may be well adapted to the fragmented nature of wetland systems. Predator density may be high for a particularly isolated wetland if landscape permeability is high and/or wetlands are important hunting grounds. Efforts should be made to determine the conditions under which isolation positively or negatively affects predator assemblage and nest predation rates.

Studies of predation in forested systems (*e.g.*, Donovan *et al.* 1997) support the hypothesis that greater forest cover and less forest fragmentation are associated with reduced nest predation and suggest that results be evaluated in the context of regional forest cover. This influence is exerted through landscape effects on predator assemblages. For example, forest fragmentation has been shown to favor predator species such as cowbirds, raccoons, crows, feral cats, and jays (Robinson *et al.* 1995). Our results exhibit a similar pattern with the probability of nest predation decreasing as percent deciduous forest cover in the landscape increased. However, both the parameter estimate and predictor weight indicated a relatively small influence.

CONCLUSIONS

Characteristics of the landscape surrounding coastal wetlands have an influence on the fate of red-winged blackbird nests within those wetlands. Nest predators interact with the characteristics of the wetlands in which they search for prey, as well as the characteristics of a specific nest site. These characteristics have a direct influence on nest predation by influencing access to those nests. However, predators also interact with the landscape surrounding these wetlands. Landscape characteristics, such as residential and commercial development, road density, and the amount of wetland cover, indirectly influence nest fate by affecting predator access to wetlands. However, few studies have directly identified predator assemblages or quantified the relationship between predator abun-

dance and landscape pattern (Chalfoun *et al.* 2002, Kuehl and Clark 2002). Geographic variation in predator assemblage, resulting from varied species pools and landscape pattern, is likely to have a significant effect on rates of nest predation (Chalfoun *et al.* 2002). Future efforts to understand nest predation in coastal wetlands should include more intensive measurements of the predator assemblages such as the use of remotely triggered camera arrays (e.g., Pietz and Granfors 2000) and emphasize the relationship between landscape pattern and predator assemblages (Chalfoun *et al.* 2002). Red-winged blackbirds continue to have potential as biomonitors of nesting productivity for birds in coastal wetlands, but additional research will be needed to establish whether other wetland nesting species respond to predation pressure in a similar fashion.

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